XV. *On the Agamic Reproduction and Morphology of* Aphis.—Part II. *By* Thomas H. Huxley, *F.R.S., Professor of Natural History, Government School of Mines. Communicated by* G. Busk, *F.R.S., F.L.S.*

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§ 1. *Embryogeny of the external organs of* Aphis.

In the previous part of this paper I sketched so much of the development of the embryo of *Aphis* as was indispensable to the clear understanding of its reproductive processes; but it appears to me that the bearings of the embryogeny of this Insect upon morphology render it worthy of a more attentive and detailed consideration.

It would be well worth while, indeed, to trace out the development of all the organs of this remarkable animal; but as I shall have for some months no leisure for labours involving so great an expenditure of time, I will content myself for the present with a notice of some of the leading features presented by the development of the external organs.

I have already stated, that one of the earliest changes in the germ of the young of the viviparous *Aphis* is the differentiation of its cellular mass into a central portion, which takes on the appearance and functions of a yelk, and which I termed "the pseudovitellus," and a peripheral coat or layer, the blastoderm. The blastoderm next becomes thickened posteriorly; and in this thickening a division takes place from without inwards, so that it is separated into a posterior flap and an anterior portion, which are only continuous dorsally. It is the flap which is the rudiment of the abdomen, while that portion of the blastoderm against which it is folded stands in the same relation to the thorax. In front of this is the rudiment of the head, constituting by far the largest portion of the blastoderm.

Dorsally and posteriorly, the rudiment of the head is originally continuous with the thoracico-abdominal thickening; but a separation early takes place at this part, and the interval is occupied by the pseudovitellus, which here comes into immediate contact with the pseudovitelline membrane.

In an embryo $\frac{1}{160}$th of an inch in length (Pl. XXXVII. fig. 5), this interval has increased so much, that the cephalic blastoderm does not extend on to the dorsal region at all, but lies almost flat under the pseudovitellus, in the anterior half of the ventral region.

In embryos $\frac{1}{140}$th of an inch in length (Pl. XXXVII. fig. 6.), I have found the cephalic portion of the blastoderm beginning to extend upwards again over the anterior face of the germ, so as to constitute its anterior and a small part of its superior wall.

This portion is divided by a median fissure into two lobes, which play an important part in the development of the head, and will be termed the "procephalic lobes." I have already* made use of this term for the corresponding parts in the embryos of *Crustacea*.

The rudimentary thorax presents traces of a division into three segments; and the dorso-lateral margins of the cephalic blastoderm, behind the procephalic lobes, have a sinuous margin.

It is in embryos between this and $\frac{1}{100}$th of an inch in length that the rudiments of the appendages make their appearance; and by the growth of the cephalic, thoracic, and abdominal blastoderm, curious changes are effected in the relative position of these regions.

In embryos about $\frac{1}{100}$th of an inch in length (Pl. XXXVIII. fig. 1, 1*a*), the procephalic lobes are so completely bent backwards as to lie close against the tergal surface of the rest of the cephalic blastoderm, so that no pseudovitelline granules can any more be seen in this region of the body. At the same time the lobes have enlarged, and extend back as far as the base of the fourth pair of visible cephalic appendages. Their infero-lateral angles are rounded and produced, forming an elevation which appears to be the rudiment of the eye.

Below the anterior extremity of the embryo, the blastoderm is produced on the median line into a tongue-like process (*lb*), whose inferior part eventually becomes the labrum, while superiorly it sends a triangular process (the rudiment of the clypeus) into the interval between the procephalic lobes.

Immediately behind the labrum, the blastoderm curves at first downwards, and then sharply upwards and backwards, to a little beyond the line of the posterior edge of the procephalic lobes.

The whole of this portion of the blastoderm belongs to the head. In the re-entering angle between it and the labrum the mouth is placed; it is a small aperture, whence the œsophagus can be traced ascending and passing backwards with a gradual curve.

Behind the cephalic region, the thoracic blastoderm passes nearly horizontally backwards, and already presents traces of a division into its three somites. Its upper surface is close to the pseudovitelline membrane, and consequently is covered by but a very thin layer of yelk-like granules.

At the end of the rudimentary thorax the blastoderm is suddenly folded forwards, so that the sternal surface of the hinder part of the future abdomen is almost in contact with that of the thorax. Having come opposite the anterior edge of the thorax, it is bent backwards, at right angles to its previous direction, for a short distance,—the extreme end being finally folded parallel with this part, and with its apex towards the head.

The great mass of the yelk lies over the abdominal blastoderm, in the space left between it and the pseudovitelline membrane. The appendages present a singular and beautiful uniformity. No trace of the pigment of the eyes is to be seen. The next anterior pair of appendages (*a t*) are more slender and elongated than the others, and are bent inwards near

* 'Lectures on General Natural History,' Med. Times and Gazette, 1856–7.

their base so as to form a sort of elbow. In consequence of this, their terminal portions are more approximated than their distal ones, and lie close together and parallel. These appendages are the antennæ; and it is worthy of remark, that they arise from the procephalic lobes, or from the point of junction between them and the rest of the cephalic blastoderm above the mouth.

Behind these and behind the mouth (though the anterior pair are very close to that aperture, and might even be described as more or less lateral in relation to it) are three pair of short, similar, conical processes. Of these the anterior pair (IV′) are the largest, and are the mandibles; the two other pairs are nearly equal: the anterior (V′) represent what are ordinarily termed the maxillæ, but which might be more properly called "first maxillæ," since the second pair (VI′), which eventually give rise to the so-called "labium," are precisely like them, and, as Zaddach (*l. c. infra*) has shown, fully deserve the title of "second maxillæ."

Three pairs (VII′, VIII′, IX′) of short processes, unjointed and not much longer than the trophi, represent the thoracic limbs.

The abdomen presents obscure traces of a division into segments.

In an embryo $\frac{1}{95}$th of an inch in length (Pl. XXXVIII. fig. 1, 1*a*, and 2), the procephalic lobes have extended so far back as completely to cover the tergal region of the head, and even to pass a little beyond the line of the last maxilla posteriorly. The fold or depression separating the thorax from the head has become deeper; the antennæ have greatly elongated, and are bent downwards and inwards, so as to meet in the middle line below, and cover the mandibles.

The first maxillæ are larger than the mandibles, and somewhat expanded at their extremities. The second maxillæ are more slender; and their bases are in a line with those of the mandibles, while those of the first maxillæ have taken a more external position. Consequently, the bases of the trophi, instead of forming two nearly parallel rows as at first, are now arranged as a hexagon, whose outer angles are constituted by the first maxillæ.

The thoracic members have greatly elongated, the hinder pair being the longest.

In embryos $\frac{1}{70}$th of an inch in length (Pl. XXXVIII. fig. 5), the blastoderm is found to have undergone a wonderful change. Instead of being folded upon itself ventrally by the flexure of the abdomen against the thorax, it has become completely extended; and so thoroughly has this extension taken place, that the abdomen is now convex inferiorly. At the same time the blastoderm has grown upwards over the sides of the body, and roofs-in its tergal region. The head is closed by the union of the procephalic lobes, and is now, in consequence of the increased length of the body, proportionally much smaller. The pigment of the eyes appears in a few scattered granules towards the posterior margin of the head on each side.

If the appendages be examined as they become metamorphosed in a succession of specimens intermediate in size between $\frac{1}{100}$th and $\frac{1}{70}$th of an inch, the antennæ are found gradually to increase in length and to become jointed. The growth of the mandibles and first maxillæ in length, on the contrary, is suspended; and they remain as short thick tubercles (Pl. XXXIX. fig. 2), from whose inner surface a long chitinous filament gradually arises. These filaments, thickening and elongating, become the blades of the mandibles and maxillæ. The growth of the second maxillæ makes up, by its excess, for the arrest of development of the mandibles and first maxillæ; for having already approximated, their confluent or connate bases elongate as one great process, which extends back in the middle line between the thoracic legs, until at length it attains more than half the length of the body, and constitutes the well-known proboscidi form "labium" of the *Aphis* *.

The thoracic members or legs have elongated so much, that their terminations are bent inwards, to allow of their lying within the pseudovitelline membrane. Their characteristic subdivisions are indicated; and the terminal claws are beginning to be formed.

From this size up to that at which the larvæ are born (Pl. XXXIX. fig. 4) (when they are less than $\frac{1}{40}$th of an inch in length), the principal changes are the following. The appendages as compared to the body, and the latter as compared to the head, undergo great elongation. The anterior pair of thoracic limbs and its somite, the prothorax, come into very close contact with the head, so that the cervical separation becomes obsolete, or is only indicated by a groove. The labrum and labium acquire their characteristic form and proportions; and the mandibular and maxillary setæ elongate, and take their final position.

The "siphons," so characteristic of the genus, appear as obtuse tubercles on the dorso-lateral region of the fifth abdominal somite. The little larva exhibits unequivocal signs of life, but still remains enclosed within its pseudovitelline membrane, to which another transparent and structureless envelope, fitting the body of the larva and all its limbs as a loose glove fits the hand, seems to have added itself. This second coat is, in fact, the embryonic integument, which is now being cast; so that the creature must undergo its first ecdysis either before, or immediately after, it is born. The head assumes its normal proportions. The corneæ become facetted; and the pigment increases greatly in amount, assuming the form of an oval deep-red patch. The clypeus and the procephalic lobes unite, but readily give way when the head is crushed, and allow of the exit of the cerebral mass, which has in the meanwhile been produced by a differentiation of the inner substance of the procephalic lobes, just as the other ganglia are the product of the blastoderm of their somites.

If the account of the development of the external organs of *Aphis* which I have just given be compared with the statements of Kölliker † and Zaddach ‡, it will be found that there is a close correspondence in all essential respects between the embryogenic phenomena of at least three orders of *Insecta*—the *Hemiptera*, the *Diptera*, and the *Neuroptera*. And, considering the universality of the law that the embryogenic processes of members of the same class have a similar fundamental character, I do not doubt that the development of all insects is, in its main features, a process similar to that described in *Aphis*.

* Zaddach considers, from his observations on *Phryganea* and other Insects, that the labium is the product, not of confluent maxillæ, but of an outgrowth of the sternum by which these are supported, the maxillæ remaining as the labial palpi. I do not deny that this may be the case in *Aphis*; but I have been unable to find positive evidence of the fact.

† De prima Insectorum Genesi, 1842.

‡ Die Entwickelung des Phryganiden-Eies, 1856.

§ 2. *Embryogeny of* Mysis *as exemplifying the* Crustacea.

But more than this, if we extend our researches into the embryogeny of the other two principal* classes of the *Articulata*, the *Arachnida* and *Crustacea*, we shall see that it presents a most remarkable agreement with that of the Insect.

To illustrate this important truth, I might cite Rathke's account of the development of *Astacus* as a type of crustacean embryogeny; but I prefer to speak from my own knowledge, and I will therefore describe the development of *Mysis*, the Opossum-shrimp.

The fertilized ova of this crustacean have a diameter of $\frac{1}{25}$th to $\frac{1}{30}$th of an inch, and consist of a yelk enclosed within a colourless and thin, but strong vitelline membrane.

The yelk is composed of two elements—small and large yelk-masses, the former having about $\frac{1}{3000}$th to $\frac{1}{4000}$th of an inch average diameter, and being usually so closely wedged together as to appear polygonal. The latter are large ($\frac{1}{1000}$th of an inch or more), spherical, and imbedded in the mass formed by the smaller kind of yelk-granules.

I was unable to detect any trace of endoplasts or cells in these ova. Acetic acid developes neither granules nor endoplasts in the yelk-masses. Upon the yelk thus constituted, the blastoderm makes its appearance as a rounded patch, which reflects the light more than the yelk, and therefore appears white by reflected, and dark by transmitted light. The contrast is greatly heightened by the addition of alcohol†, or of acetic acid. When the latter reagent has been employed, or even before, if the examination be very carefully conducted, the structure of the blastoderm is seen to be widely different from that of the rest of the yelk. No yelk-granules are visible in it, but it appears to be very finely granular; and imbedded within it are numerous close-set vesicular endoplasts, having a diameter of $\frac{1}{1800}$th to $\frac{1}{2000}$th of an inch. These usually contained many granules, sometimes only one; but I cannot say I have been able to detect any definite nucleolus in them.

The discoid blastoderm is thickest in its middle region, thinning off gradually on both sides, and internally is sharply defined from the substance of the vitellus. In the centre it exhibits a more or less marked depression. As development goes on, this depression becomes more and more marked, while the disk thickens and increases circumferentially. At the same time, the layer of yelk in immediate contact with the disk, and co-extensive with it, is found to have a somewhat different constitution from the rest. The globules are large, dark, and sharply defined, and acetic acid gives them a granular appearance, but developes no endoplast.

The depression above alluded to now increases, so as to form a fissure which separates a small tongue-shaped process from the rest of the blastoderm, to which it nevertheless remains closely applied. This process is the rudiment of the abdomen, and in a front view it is rendered more distinct by several clear lines, which mark the commencement

* I have no doubt that the *Myriapoda* will be found to exemplify the same morphological laws, with the exception of that relating to the total number of somites in the body, as their congeners; but I find so much that is unsatisfactory in the existing accounts of their development, and so many points in their anatomy requiring re-investigation, that I prefer for the present to be silent about them.

† Rathke, in his numerous embryological researches, appears to have constantly availed himself of this property of alcohol in order to render the blastoderm more distinct.

of the future caudal bristles. In front of the end of the abdominal process, two minute conical prominences, at first marked by similar, but fewer clear striæ, gradually raise themselves up on each side from the surface of the blastoderm and elongate, their apices being directed backwards. They are the rudiments of the antennules and antennæ.

A delicate structureless membrane is now visible, covering these parts and the adjoining portions of the germinal membrane. It is produced into the terminal setæ of the end of the abdomen and of the two pairs of appendages, and is the commencement of the first skin of the larva*.

The anterior part of the blastoderm is wider than the posterior, and is produced into two great lobes divided by a median fissure. These are the "procephalic lobes," and have the same relation to the anterior division of the head as the corresponding parts in the embryo *Aphis*.

In this state the embryo becomes a larva, for it bursts its vitelline envelope and lies naked in the pouch of the mother. The rudimentary abdomen is at the same time extended, so that the little creature is now about $\frac{1}{20}$th of an inch in length, and is very like a pear in shape, the stalk being represented by the abdomen, which is terminated by a flattened, bifid, spinulose fin.

The whole larva is covered by a continuation of the delicate membrane already noticed on the limbs and abdomen. The blastoderm invests the abdomen almost completely, but in front it covers only a somewhat fiddle-shaped area on one face of the yelk. It is still more deeply bilobed in front, and the antennules and antennæ are much elongated. The larva next begins to grow, being doubtless nourished by the fluid contained in the maternal pouch; and at the same time its ventral region assumes a curve, contrary to that which it originally possessed, becoming more and more convex.

The cephalic region is now clearly distinguishable; it occupies nearly one-half of the whole length of the body. The procephalic lobes extend upwards over the anterior face of the vitellus, and upon each a large rounded elevation, the rudiment of the ophthalmic peduncle, has made its appearance in front of the antennule. The latter, like the antennæ, elongate greatly, and become divided longitudinally, within the sheath afforded by the primitive integument, into their two terminal branches.

A slight constriction indicates the boundary between the antennulary and antennary sterna, and behind these, similar depressions mark off the surface of the blastoderm into seventeen additional segments.

Attached to them are as many pairs of appendages, which in the youngest larvæ examined had the following form:—

The first pair were rounded massive elevations, situated one on each side of the pit indicating the position of the oral aperture; from their anterior edge a short oval palp already projects. These are the rudimentary mandibles.

The next pair, or first maxillæ, are small rounded elevations meeting in the middle line. The second maxillæ succeed, and are more elongated, three-jointed, and bent back parallel with one another. The maxillipedes and the thoracic ambulatory legs form one continuous

* See, for illustrative figures of the development of *Mysis*, my 'Lectures' above cited.

series of similar appendages, all elongated and bent back against the sternal surface of the body.

The abdomen is very short, but is clearly distinguishable from the thorax by its less complete segmentation, and by the rudimentary condition of all its appendages save the last pair.

The blastoderm as yet extends only for a little way on the sides of the body. The primitive larval integument still invests the whole body loosely, but passes smoothly over all the appendages, except the antennules and antennæ, which continue to be ensheathed by it.

The larva remains in this general condition until it attains $\frac{1}{14}$th of an inch in length, the principal differences in its later stages being the increased growth of the body as compared with the head, the completion of the dorsal surface by the upward extension of the blastoderm, and the gradual restriction of the yelk to the anterior part of the body.

I have been unable to determine, as precisely as in *Aphis*, the exact share taken by the procephalic lobes in the composition of the roof of the head in the crustacean; but they assuredly extend over a considerable part of its latero-dorsal parietes.

The carapace appears at first as a ridge-like process developed from the dorso-lateral region of the antepenultimate and preceding thoracic and cephalic somites, as far forwards as the bases of the antennules. It is certainly not an extension backwards of the terga of any of the anterior cephalic somites, but is from the first continuous with, and developed from, the thoracic somites.

It is needless to trace the history of the larval *Mysis* further,—what has been said sufficiently proving the close resemblance of its development to that of *Aphis*.

§ 3. *Embryogeny of* Scorpio *as exemplifying* Arachnida.

I have not yet had the opportunity of working out the development of an Arachnidan; but the researches of Rathke* and Herold† are so full and clear, that the omission is of little moment.

Rathke's observations on the development of the Scorpion show that after, or even before, the blastoderm has extended over the whole yelk, a papillary elevation appears at one pole. It is the rudiment of the future abdomen, including under that term all the segments of the body behind that which carries the last pair of respiratory organs. In front of this, eleven pairs of closely approximated thickenings make their appearance; and then, at the sides of the sixth to the tenth pair of them, inclusively, counting from the rudimentary abdomen, papillary processes are developed. It is clear, from Rathke's figures, that the anterior pair of thickenings are the "procephalic lobes," while the succeeding ones are the sterna of the somites between the mouth and the abdomen. The five pairs of processes thrown out by the five anterior of these are the great chelæ and the four pairs of ambulatory appendages. The antennæ make their appearance subsequently from the procephalic lobes (or their junction with the rest of the blastoderm) in front of the mouth. It is not expressly stated, but I do not doubt, from Rathke's figures, that the upper region of the head is formed, as in *Insecta* and *Crustacea*, by the union of these lobes.

* Reisebemerkungen aus Taurien, 1837.

† De Generatione Aranearum, 1824.

Rathke's account of the number of rudimentary post-oral sterna would lead one to suppose that in the embryo one sternum is wanting. I believe, however, that the truth is, that the sterna of the genital and pectiniferous somites were already so much smaller than the rest in the embryos which Rathke chanced to examine, as to be regarded by him as one.

I base this conclusion upon the condition of the nervous system, which consisted of eleven pairs of clearly distinguishable post-oral cephalo-thoracic ganglia; that is, of just the same number as in an embryonic *Astacus*. Of these, the four posterior were widely separated, and lay in the pulmoniferous somites; while the seven anterior pairs extended only a little way beyond the ambulatory appendages, and were united into a triangular mass. The anterior of these ganglia were the largest, the posterior the smallest. The anterior pair gave off the nerves to the chelæ.

It would be difficult to obtain a more clear and conclusive proof than this, that the chelæ of the Scorpion are the homologues of the mandibles of the Crustacean, and that the succeeding somites, as far as the last pulmoniferous one, correspond with the fifth to the fourteenth somites, inclusively, of the typical Crustacean. The six succeeding somites are the homologues of the six abdominal somites of the Crustacean; the aculeated sting corresponds with the telson; and the only difference presented by the pre-oral somites is that common to all air-breathing *Articulata*, viz. the sessile eyes, and the non-development of one of the pairs of antennæ.

§ 4. *Generalizations regarding the Embryogeny of the* Articulata, *and Morphological Laws based on these.*

From all these facts of development, I deduce the following morphological laws (some of which have already been enunciated for particular classes) for the *Articulata* (*Insecta*, *Arachnida*, *Crustacea*) generally.

1. The first-formed rudiment of the embryo corresponds with its sternal surface, or with the side upon which the great centres of the nervous system are placed. It is a neural rudiment.

2. In the thorax and abdomen this neural rudiment grows up on each side towards the tergal region, or that on which the great centre of the circulation is placed.

3. In the Articulate embryo, therefore, the neural wall is formed first, and gradually extends tergally so as to form the hæmal wall.

4. The cephalic blastoderm very early undergoes a peculiar flexure, a greater or less portion in front of the mandibles being bent up at right angles to the rest, and even in many instances extending backwards, so as to constitute the entire hæmal region of the head. In these cases the top of the head is in reality a sternal, and not a tergal, surface.

As a consequence of this flexure, the line of attachment of the bases of the eyes and antennæ is frequently altogether above that of the other appendages, so that they appear to be tergal, and not sternal, appendages.

5. The anterior extremity of the cephalic blastoderm becomes early divided by a median fissure, each lateral portion being a "procephalic lobe." In Insects the line of junction of these procephalic lobes is the epicranial suture.

6. In *Insecta* and *Crustacea* the head, in the embryo, is easily distinguishable from the rest of the body. In Podophthalmous *Crustacea* it is clearly seen to be composed of six somites, each possessing a pair of appendages; of these, the first are the eyes; the second, the antennules; the third, the antennæ; the fourth, the mandibles; the fifth, the first maxillæ; and the sixth, the second maxillæ.

In *Insecta*, on the other hand, only four pairs of appendages appear in the head, the eyes being sessile, and one pair of antennary organs remaining undeveloped.

In the *Arachnida* it appears to me to be quite clearly shown by development that the anterior pair of appendages are antennæ; the second pair, mandibles, with a hugely developed palpus; the third pair, first maxillæ; and the fourth pair, second maxillæ, converted, like the next two pairs of appendages, into ambulatory legs.

It follows, therefore, if we take the number of moveable appendages as the test, that in the *Articulata* never more than six, and never fewer than four somites enter into the composition of the head. But is the number of moveable appendages a just test of the number of somites entering into a part? No one will pretend that it is so in the abdominal and thoracic regions; and if we consider the head of *Crustacea* alone, we find the eyes becoming sessile, and one pair of antennary organs aborting, without the least reason for concluding that the typical structure of the head is altered. It seems to me, then, hardly a hypothesis to assume that the sessile eyes of Insects represent the appendages of a somite, since it is universally admitted that they do so in *Edriophthalmia*. But by this assumption we arrive at a still closer approximation of the different classes in regard to their cephalic structure; for all would, on this supposition, have either five or six cephalic somites,—the former number being invariably met with in the true air-breathers (though in many purely aquatic forms also), while the latter is found only in those which respire by means of gills.

I repeat, I can see nothing in this generalization but a simple expression of the facts. But I would go a step further, and add to this the *hypothesis*, that in the *Articulata* the head is normally composed of six somites, which are all fully developed only in *Podophthalmia*, *Stomapoda*, and some *Branchiopoda*; while in other *Crustacea*, some one or more of the pre-oral somites is more or less abortive, and in *Arachnida* and *Insecta*, the appendages of the first somite are sessile, and those of the second or third undeveloped. Admitting this hypothesis, I find further, that of the six cephalic somites, the sterna of three (the mandibular and two maxillary) are always situated behind the mouth and on the ventral surface of the body. The position of the other three varies; but the most anterior or ophthalmic is always bent upwards in consequence of the cephalic flexure, and not unfrequently, as in Insects, constitutes the greater part, or the whole, of the dorsal region of the head. The next two, or antennulary and antennary sterna, may present every variation from approximative parallelism with the axis, in *Squilla*, to extreme reflexion, as in *Insecta* and many *Crustacea*.

7. Nothing can be more variable than the number of the somites whence appendages are developed in the various classes and orders of the *Articulata*; and in the *Myriapoda* the total number of somites even is susceptible of an extreme amount of variation. But in the other classes it appears to me that there is a typical number of somites, from whence

but comparatively few forms depart either by way of excess or defect. Thus, if we leave out the *Læmodipoda*, all Podophthalmous and Edriophthalmous *Crustacea* have twenty somites, of which six are cephalic, eight thoracic, and six abdominal. In a very few *Branchiopoda*, and in *Trilobita*, there is more than the typical number of somites; but I believe that in all other *Crustacea*, where the number of somites is not twenty, it is less.

The question of the typical number of somites in the body of the *Insecta* is one which has been much discussed. But all the theories on this subject with which I am acquainted are, in my apprehension, vitiated by the mistaken view which their authors take of the composition of the Insect's head. Many seem to consider it to be a simple segment; while those who admit a multiplicity of segments, appear to be misled by the position of the eyes and antennæ, into regarding them as tergal appendages of the segments over whose sternal appendages they lie—as a kind of wings of the cephalic somites, in short. Again, it is supposed by many that the labrum and the lingua are the representatives of the appendages of distinct somites, a conception which is at once negatived by the study of their development.

As I have endeavoured to show, there are certainly five, and hypothetically six, somites in the head of *Insecta*; there are certainly at least three in the thorax; but the number in the abdomen has been as much disputed as the number in the head. Zaddach considers, as a general rule, ten to be the number of abdominal somites in Insect larvæ; Westwood and Newport enumerate eleven in some *Hymenoptera*, and this last is, I believe, the maximum number of somites which has yet been found in the abdomen. Now, if we assume the number of somites in the head to be six, the number in the thorax three, and the number in the abdomen eleven, we shall arrive at twenty as the maximum number of somites in the body of an Insect.

This conclusion is in remarkably close accordance with the results obtained by M. Lacaze-Duthiers from his laborious and remarkable researches into the structure of the female genital apparatus of *Insecta*. M. Duthiers finds that the vulva always opens between the eighth and ninth abdominal somites, and that in *Neuroptera*, in *Orthoptera*, in most *Hemiptera*, and in *Thysanura*, three somites intervene between the vulva and the anus, which is always placed at the very extremity of the body. There are thus eleven abdominal somites, and, therefore, a total number of twenty, in these four orders.

Some *Hemiptera* have the last abdominal somite abortive, and this appears to me to be the case in *Aphis*. In *Coleoptera* and *Hymenoptera*, the tenth and eleventh somites abort, nine only remaining: in *Lepidoptera*, finally, all three post-genital somites remain undeveloped. M. Lacaze-Duthiers' researches tend to show that a fundamental unity prevails amidst those apparently most diverse apparatuses which we know as stings, borers, and ovipositors, and that they are always the result of a modification undergone by the ninth abdominal somite.

I do not consider myself competent to give an opinion as to the details of the investigations to which I have just alluded, but I cannot refrain from expressing the belief that the labours of future investigators will bring only a confirmation of their general accuracy.

The only adult Insect, besides *Aphis*, which I have studied with sufficient care in reference to these views, is the common Cockroach (*Blatta orientalis*), an insect which I can recommend as admirably adapted for investigation. Here it is very easy to find the eleven abdominal somites, and to satisfy oneself that the vulva is placed between the eighth and ninth, and that the two outer elongated pieces of the curious clasping apparatus for the ovisacs are formed by a modification of parts of the ninth somite. The smaller and inner processes, on the other hand, are clearly developed from the sternum of the tenth somite, while the lateral anal valves represent the eleventh somite.

I have found that while the vulva opens between the eighth and ninth somites, the aperture of the spermatheca is situated on the sternum of the ninth, and that of the colleterial glands on the sternum of the tenth somite.

In the male the complex penis is formed by a modification of the tenth somite, and the aperture of the vas deferens is on the sternum of this somite, or between it and the eleventh.

Weighing all these facts, the conclusion to which they point seems obvious, viz. that in *Insecta*, as in *Crustacea*, the typical number of the somites is twenty.

I have shown above that the development of the Scorpion proves that there are seventeen post-oral somites besides the sting (which is plainly the homologue of the telson in the *Crustacea*) in this Arachnidan. If we make the same assumption for the Scorpion as for the Insect, that one of the antennary somites is abortive, we shall have a total of twenty somites here also. The anatomy of the adult Scorpion appears to me fully to confirm this view. Beginning at the hinder end, we find, including the telson, six segments behind those which carry the respiratory apertures. Of these there are four; and in the three posterior, the sternum has nearly the same length as the tergum; but in the anterior one the sternum is much longer than the tergum. Furthermore, these sterna at first seem to occupy the whole space up to the posterior boundary of the cephalothorax, while, on the dorsal side, two narrow terga lie between the tergum corresponding with the anterior sternum and the cephalothorax.

It appears, therefore, as if there were two more terga than sterna in the abdomen; but on more careful investigation, the missing sterna show themselves as the supports of the pectines and of the genital aperture in front of these last curious organs. Indications of the terga which belong to the two posterior pairs of ambulatory limbs are clearly visible on the posterior part of the cephalothorax, and these limbs are strongly distinguished from the anterior two pairs by the absence of the triangular processes directed towards the mouth, which characterize the bases of the latter. Indeed, the anterior ambulatory legs, by means of these processes, take part in the formation of the oral cavity as completely as do the maxillæ of any other Articulate animal.

Another exceedingly natural demarcation between the two anterior and two posterior pairs of ambulatory limbs is afforded by the so-called 'diaphragm' which divides the thoracic from the cephalic cavity, and whose attachment corresponds with the interval between these two sets of appendages.

In *Galeodes*, the two posterior pairs of ambulatory legs are attached to distinct segments.

There is no necessity to enter into any disquisition upon the homology of the appendages and the general uniformity in plan, so far as the anterior part of the body is concerned, in all *Arachnida*. But it may be asked, what becomes of the hinder thoracic and the abdominal somites in the Spiders and Mites? Without, at present, giving a positive answer to this question, I am inclined to think that the Spiders stand to the Scorpion in the relation of *Læmodipoda* to *Amphipoda*, and that many of their posterior somites are aborted.

I do not doubt that many minor variations will be detected when the morphology of the *Articulata* is carefully examined; but I venture to think it a result of no small moment, if it can be proved that a Lobster, a Cockroach, and a Scorpion are composed of the same primitive number of somites; that the head in each consists of the same number of parts, and that the great differences are the consequence of the different modification of the thoracico-abdominal somites, all fourteen of which bear appendages in the Lobster, while only three (or if we consider the genital apparatus in the light of appendages, five) are so provided in the Insect, and only two (leaving out of consideration the "pectines") in the Scorpion.

8. I have elsewhere* explained at length my views with regard to the nature of the carapace in the *Crustacea*, and I will only repeat here, that there seems to me to be no constancy in its composition. The rudimentary carapace of *Squilla* is assuredly developed from not more than four somites, the antennary, mandibular, and maxillary. In *Apus*, I doubt whether more than the six cephalic somites enter into its composition. In *Cuma* it is constituted by the cephalic and three anterior thoracic somites, in *Mysis* by the cephalic and six or seven anterior thoracic, and in ordinary *Podophthalmia* by all the cephalic and thoracic somites.

9. Lastly, there are certain parts developed singly in the median line in the *Articulata*. Of this nature are the frontal spines of *Crustacea*, their telson, and the sting of the Scorpion, whose mode of development appears to be precisely similar to that of a telson. In the same category we must rank the labrum in front of the mouth, which in the *Crustacea* (at least) appears to be developed from the sternum of the antennary or third somite, the metastoma (or so-called labium or lingua) of *Crustacea*, and the lingua of *Insecta*, behind the oral aperture.

However much these appendages may occasionally simulate, or play the part of, appendages, it is important to remember that, morphologically, they are of a very different nature, and that the confusing them with true appendages must tend completely to obscure the beautiful relations which obtain among the different classes of the *Articulata*.

§ 5. *The Embryogeny of the* Articulata, Mollusca, *and* Vertebrata *compared.*

I find it difficult to conclude this memoir without saying a few words on the resemblances and differences between the embryogenic changes of the *Articulata* and those of the *Mollusca* and *Vertebrata*. Absolute and fundamental differences appear to me to separate the members of these three classes almost from the first appearance of the germ.

As we have seen, it is the neural side of the Arthropod which is first developed, while, so far as I am aware, it is the opposite or hæmal side which is first formed in every

* "Lectures," Med. Times and Gazette, 1857.

Mollusk. The germ of the Arthropod becomes antero-posteriorly segmented; the germ of the Mollusk never does so. From these two fundamental differences a multitude of others necessarily follow.

The Articulate embryo is no less markedly separated from that of a Vertebrate animal, although in the latter, as in the former, it is the neural surface which is first developed; for I know of nothing in the Articulate embryo to be compared with the primitive groove, the chorda dorsalis, and the dorsal plates of the Vertebrate*. They, like the amnion and the allantois, are, I believe, structures without a representative in the other two sub-kingdoms.

There is perhaps, as Zaddach maintains, a certain analogy between the primitive segments of the Articulate animal and the primitive vertebræ ("Urwirbel" of Remak) in the Vertebrate, but with the commencing differentiation into tissues the resemblance entirely ceases. The appendages of the Vertebrate embryo are more Molluscan than Articulate in their primitive mode of development. Notwithstanding all these great and real differences, however, there appears to me to be one respect in which a most singular analogy obtains between the Vertebrate and the Articulate type:—it is in the construction of the head.

Adopting, in some respects, the views of Prof. Goodsir†, I can recognize at least six more or less complete segments in the completely ossified Vertebrate cranium. It is clear that the Vertebrate mouth opens like that of the Articulate animal, though on the opposite side of the body, between an anterior and a posterior set of cephalic segments. In the interior of the cranium a no less natural boundary between the anterior and the posterior set of cephalic segments is afforded by the pituitary body and its fossa, when the latter exists.

I find, again, in the cranio-facial bend of the base of the cranium in the Vertebrate embryo, something wonderfully similar to the cephalic flexure of the Articulate head, and in the cranial trabeculæ (Schädel-balken of Rathke), analogues of the procephalic lobes.

While fully recognizing the fundamental differences between the Articulate and the Vertebrate type, then, I think we should greatly err if we overlooked such singular analogies as these. Future research will show whether they are or are not the outward signs of a deeper internal harmony than has yet been discerned, between the *Articulata* and *Vertebrata*.

Since the present memoir was read to the Society, some additional facts of importance have come to my knowledge. In the first place, my friend Mr. Lubbock, having undertaken to work out the development of *Coccus*, was led thereby to search for what I have called "ovarian glands" in other insects. His results will be published at length elsewhere; but he permits me to say that corresponding organs exist in all *Lepidoptera*, *Hymenoptera*, Geodephagous and Hydrodephagous *Coleoptera*, *Diptera*, and most *Neuroptera*, while they are absent in *Orthoptera*, *Pulex*, *Libellulidæ*, &c., and are all terminal,

* I therefore by no means agree with what Zaddach says on this subject, or with regard to the homologue of the amnion in *Articulata*.

† As expressed in the Edinburgh New Philosophical Journal, 1857, p. 118 *et seq.*

instead of forming groups between the egg-germs, in the non-geodephagous *Coleoptera* and *Hemiptera*. They have been figured in *Lepidoptera* by Herold, Meckel, Thompson, and Stein, in *Diptera* by Stein and Leuckart, and in *Coleoptera* by Stein.

Secondly. In September last I received the fourth Part of the fourth volume of Moleschott's 'Untersuchungen,' which contains a long and remarkable Essay by Leuckart, "Zur Kenntniss des Generations-wechsels und der Parthenogenesis bei den Insekten." The first article in the memoir is on the "Alternation of Generations in the *Aphides*." The author describes at length, and figures, the female reproductive organs of *Aphis Padi*; and although the arrangement of these organs is somewhat different from what obtains in my *Vacuna*, I am happy to say that his account of the ultimate structure of the ovaries essentially coincides with mine. The view which Leuckart takes of the relation of the ova and agamic germs (p. 346) is also in close agreement with my own. I lay the more weight upon these coincidences because Prof. Leuckart's observations must have been made at the same time with, and were of course wholly independent of, mine.

Lastly, not having the works of either Kaltenbach or Koch at hand when my memoir was read, I abstained from attempting to give the specific names of my *Aphides*. I have no doubt now that the viviparous form is the *Aphis Pelargonii* of Kaltenbach, especially as my friend Mr. Dallas, who has paid particular attention to the *Hemiptera*, is of that opinion. The oviparous female resembles so much in form and habit the *Vacuna dryophila* of Schrank, that I have little doubt it is really that species, though, when carefully examined, the antennæ are found to have six unquestionable joints, and seven, if the swollen base of the last division of the antenna is to be regarded, as I believe it should be, as a distinct joint. The eyes also have a small and inconspicuous tubercle; and the promuscis is not nearly so long as either Kaltenbach or Koch states.—*Nov.* 16, 1858.

DESCRIPTION OF THE PLATES.

Tab. XXXVI.

Aphis Pelargonii.

The letters have the same signification throughout. The fractions indicate the measured size, in parts of an inch, of the objects.

Fig. 1. The three anterior chambers of a pseudovarium: A. the apical chamber; B. the second; C. the third. *a.* Pseudovarian ligament; *b.* wall of the pseudovarium; *c.* its epithelium; *d.* periplast or homogeneous matrix of the apical chamber; *e.* clear vesicle; *f.* its endoplast, the two corresponding with the germinal vesicle and spot of an ovum; *g.* a pseudovum partially detached, its periplast greatly enlarged; *e′.* its vesicle, whose endoplast is invisible; *h.* blastoderm; *i.* pseudovitellus.

Fig. 2. Terminal chamber of a pseudovarium, with the second chamber beginning to be formed in

consequence of the enlargement of the pseudovum (*g*), which is about $\frac{1}{960}$th of an inch in diameter.

Fig. 3. The pseudovum is still more enlarged, and the second chamber is nearly distinct. The vesicle, *e*′, remains, and exhibits certain indistinct granules in its contents. The cells of the blastoderm of c measure about $\frac{1}{2500}$th of an inch in diameter.

Fig. 4. The second chamber is quite distinct from the first, and contains a mass (*g*) in which no clear vesicle could be discovered: this mass became clearer and irregularly areolate by the action of water.

Fig. 5. The cellular germ-mass. The cells or clear cavities have a diameter of about $\frac{1}{3200}$th of an inch; their endoplasts are hardly more than $\frac{1}{10000}$th of an inch in diameter.

Tab. XXXVII.

Aphis Pelargonii. Letters as before.

Fig. 1. A portion of the blastoderm and pseudovitellus of an unaltered germ, only $\frac{1}{386}$th of an inch in length, but otherwise like the preceding. The clear vesicles measured $\frac{1}{3200}$th of an inch; the endoplasts $\frac{1}{18000}$th.

Fig. 2. A germ extracted from its chamber and treated with acetic acid. It has no pseudovitelline membrane.

Fig. 3 *a*. A germ extracted from its chamber. It is enclosed within a pseudovitelline membrane (*k*); and its pseudovitellus is arranged in obscure spheroids, of which one is represented in 3 *b*. acted on by water. Its granules are about $\frac{1}{9000}$th of an inch in diameter.

Fig. 4. Germ $\frac{1}{215}$th of an inch in length. The cells of the posterior end (3) present a sort of break (*l*), and the blastoderm on one side is greatly thickened. The thickened portion offers an indication of a division (*m*). The anterior end (*y*) is also somewhat thickened.

Fig. 5 *a*. Germ $\frac{1}{160}$th of an inch, enclosed within its pseudovitelline membrane: *n*. rudiment of the abdomen; *o*. of the thorax; *p*. of the head; *l*′. gap corresponding with *t*, and now filled by the pseudovitellus; *q*. inner layer of the germ; *r*. that portion of it which will become the pseudovarium. 5 *b*. Diagrammatic view of the same, viewed from above.

Fig. 6. Lateral view of a larger germ without its pseudovitelline membrane. The anterior part of the cephalic blastoderm (*p*) has extended upwards, and constitutes the procephalic lobe *p*′. The rudiment of the pseudovarium (*r*) is still more distinct than in the preceding.

Tab. XXXVIII.

Aphis Pelargonii.

Fig. 1. Embryo enclosed within its pseudovitelline membrane. The pseudovitellus has aggregated over the abdomen, and more or less completely left the thorax. Letters as before, except—*s*. the first larval integument; *lb*. labrum; *at*. antenna; IV′. mandible; V′. first maxilla; VI′. second maxilla; VII′. first, VIII′. second, and IX′. third thoracic leg. 1 *a*. The same embryo seen from below.

Fig. 2. Embryo of the same size, viewed from below and the side, the blastoderm unfolded, and the appendages separated.

Fig. 3. Highly magnified view of part of the pseudovitellus, and of the rudiment of the pseudovarium, in an embryo $\frac{1}{90}$th of an inch in length.

Fig. 4. Embryo $\frac{1}{84}$th of an inch, enclosed in its pseudovitelline membrane.

Fig. 5. Embryo $\frac{1}{70}$th of an inch, in its pseudovarian chamber.

Tab. XXXIX.

Aphis Pelargonii.

Fig. 1. A. Nearly full-grown fœtus, extracted from its investments, and somewhat unfolded: *t*. anus, whence the alimentary canal is seen taking a curved S-like course to the mouth. B. Terminal chamber of one of the pseudovarial cæca of this embryo.

Fig. 2. The mouth of this embryo seen from below. The "labium" (VI′) already appears as a large single process bilobed at its free end.

Fig. 3. Side view of the head of a similar embryo, showing the relative position of the different appendages and the course of the œsophagus.

Fig. 4. A nearly full-grown fœtus in its pseudovitelline membrane: I′. the pigment of the eye; *s*. rudimentary siphons.

Fig. 5. A partially diagrammatic figure of the wingless viviparous form of *Aphis Pelargonii*. The Roman numbers indicate the typical somites of the body and their appendages; the other numbers mark the abdominal somites. A. Anus; G. genital aperture; S. siphon.

Tab. XL.

Reproductive Organs of the oviparous Aphis (*Vacuna dryophila*).

Fig. 1. The female organs entire. One ovarian cæcum only is represented; and I have purposely selected one of those, the ovarian glands in whose apical chamber are very similar, at first sight, to ova. A. Anus; B. vulva; C. vagina; D. oviducts; E, F, G, H, I, K. chambers of the ovary; L. ovarian glands; *m*. colleterial glands; *n*. spermatheca; 7, 8. seventh and eighth abdominal sterna.

Fig. 2. The three anterior chambers of an average ovarian cæcum. Letters as before, with the addition of—*o*. germinal vesicle of the nascent ova in the terminal chamber (K); *o*′. germinal vesicle of ovum in I; and *o*″. of ovum in H; *p*. epithelium; *q*. cord-like secretion of ovarian gland, *l*; *l*′. inner capsule of ovarian gland.

Fig. 3. The end of another ovarian cæcum, showing very distinctly the apparent continuity of the cord, *q*, with the ovum in the third chamber. The granules of the viscid vitelline mass (which is surrounded by no membrane) are so numerous as to hide the germinal vesicle.

Fig. 4. A. Posterior extremity of the ovum unaltered: *r*. chorion; *s*. tubercular elevation; *t*. appendage; *u*. its gelatinous investment; *v*. rod-like bodies imbedded therein; *v*′. the same more magnified. B. Anterior end of the ovum after the action of potash; *y*. papillary elevation; *z*. internal markings of the chorion (*r*); *w*. vitelline membrane; *x*. vitellus. C. Posterior extremity treated in the same way: *s*′. micropyle?